

Obs. — Les exemplaires de l'Europe orientale se rapportent à *candidatus* Pall., ceux du Nord-Africain à *albotesselatus* Fairm. (*Lucasi* Chevr.), d'Espagne et Baléares à la ssp. *tesselatus* Fairm., de France à la var. *Abeillei* Chevr.

Le type du *tesselatus* Fairm. provient d'Andalousie, celui d'*albotesselatus* Fairm. de Constantine, du *tesselatus* Lucas des environs de l'oasis de Laghouat. La var. *Abeillei* se distingue par sa forme plus étroite et la présence d'une fossette frontale distincte, alors que celle-ci n'est représentée que par un point plus ou moins visible (ou absent) chez les autres formes.

An outline of the Phylogeny of the *Formicidae*

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Though much work has been done on the phylogeny of the *Formicidae*, a great deal of confusion exists, owing to the disagreement of those best qua-

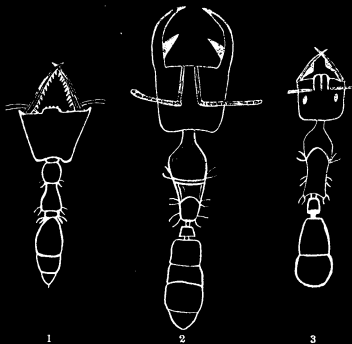


Fig. 1. — *Mystrum Voeltzkowi* ♀ (after HEINRICH).

Fig. 2. — *Dorylus* (*Anonema*) *nigricans* Ill. ♀ var. *moesta* Sants.

Fig. 3. — *Plectroctena mandibularis* ♂m. ♀.

lified to judge the correctness of the different theories put forward. Before making a more detailed study of the phylogeny of the *Formicidae*, it is necessary to decide, taking into account the physiological features of each sub-

family, in what manner, and from what base, each sub-family has evolved. Unfortunately it is here that the greatest confusion exists.

EMERY believed that the *Dorylinae* Schuckard was the oldest sub-family; in this, he disagreed with both FOREL and WHEELER, the two greatest workers on this subject, who believed that the *Ponerinae* Mayr was definitely the oldest sub-family, from which all the other sub-families were descended. I do not think that there can be any doubt, that this latter theory is correct. It is true that there is a missing link between the *Ponerinae* and the *Mutillidae*, from which that sub-family is supposed to be directly descended; the Ponerine genus *Mystrum*, however, all but supplies that link (see fig. 1); in fact, as reported by FOREL, HENRI DE SAUSSURE insisted that the ♂ of *Mystrum Voeltzkowi* was a Mutillid. I feel justified therefore in taking the primitive *Ponerinae*, as represented by the genus *Mystrum* Roger, for the base of our phylogenetic tree.

Now, FOREL believed that the *Dorylinae* were descended from the *Ponerinae*, through the *Cerapachyinae*. The *Cerapachyinae* were classed, originally as one of the primitive tribes (*Cerapachii*) of the *Ponerinae*, but the tribe was raised to a sub-family by WHEELER in 1922. Taking into account the anatomical resemblance of the *Cerapachyinae* and the *Dorylinae*, on one hand, the *Cerapachyinae* and the primitive *Ponerinae* on the other hand, also the fact that the *Dorylinae* (see fig. 2) definitely, I think, finished their development into a separate sub-family, by the end of the Mesozoic (in this latter statement I am in agreement with EMERY), I consider FOREL to be correct.

WHEELER points out that the following genera are common to both the Australian and European faunas, which were separated during the Eocene, and concludes that we are justified, therefore, in considering them of Mesozoic age:

- **Cerapachys*,
- **Platythyrea*,
- **Ectatomma*,
- **Euponera*,
- **Ponera*,
- **Anochetus*,
- Sima*,
- **Monomorium*,
- **Cardiocondyla*,
- **Aphaenogaster*,
- **Tetramorium*,
- **Strumigenys*,
- **Epilritus*,
- **Dolichoderus* (S. g. *Hypoclinea*),
- **Iridomyrmex*,
- **Bothriomyrmex*,

- Oligomyrmex*,
- **Cremastogaster*,
- **Pheidole*,
- **Solenopsis*,
- Vollenhovia*,
- Podomyrma*,
- **Myrmecina*,
- **Tapinoma*,
- Technomyrmex*,
- Plagiolepis*,
- Acantholepis* (S. g. *Stigmatoceros*),
- Pseudolasius*,
- Oecophylla*,
- **Prenolepis*,
- **Camponotus*.

Also the following genera, together with those in the above list which are marked with an *, are common to the Australian, Neartic and Neotropical faunas :

Sphinctomyrmex,
Acanthoponera,
Lepogenys,

Odontomachus,
Rogeria.

These, for the same reason, must be of Mesozoic age.

It will be seen that approximately 67 % of these genera belong to the sub-families *Ponerinae*, *Cerapachyinae*, *Pseudomyrmicinae* and *Myrmicinae*. Also that only 16 : 6 % belong to the *Formicinae*.

Now approximately 65 % of the ants in the above lists, all of which are



Fig. 4. — Poison apparatus of *Plectroctena mandibularis* (sm. ♀).

Fig. 5. — Poison apparatus of *Bothriomyrmex meridionalis* (after FOREL).

Fig. 6. — Poison apparatus of *Formica rufibarbis* (after FOREL).

of Mesozoic age, belong to the sub-families *Myrmicinae*, *Pseudomyrmicinae*, *Dolichoderinae* Forel, and *Formicinae*, which are descended, directly, or indirectly (FOREL and WHEELER agree on this) from the *Ponerinae*. Therefore we can safely conclude, as does, WHEELER (though apparently not for this reason) that the *Ponerinae*, i. e. the first of the *Formicidae*, appeared earlier than was thought, probably in the Triassic or Jurassic. That is that the differ-

rentiation of the sub-families started in the early Mesozoic. Thus we have decided that the development from the primitive *Ponerinae* to the *Dorylinae*, through the *Cerapachyinae*, started in the early Mesozoic, and was possibly, if not probably, finished before the end of the Mesozoic Age.

At the same time, of course, the main branch of the *Ponerinae* was continuing to develop (see fig. 3).

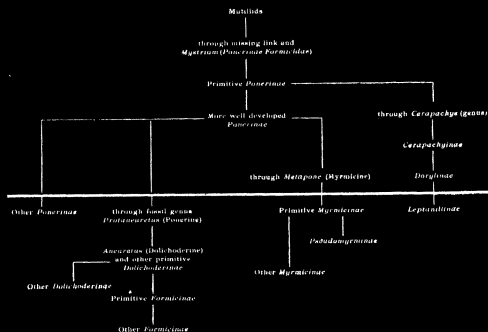
FOREL believed that the *Formicinae* were directly descended from the *Ponerinae*; though this seems possible, owing to external anatomical resemblance, I cannot agree. If one studies the poison apparatus of the sub-families *Ponerinae*, *Dolichoderinae* and *Formicinae*, one finds that a process of deterioration takes place, from the well developed apparatus in the *Ponerinae* through the *Dolichoderinae*, to the very much atrophied organ found in the *Formicinae* (See fig. 4, 5, 6). It would be impossible for the poison apparatus of the *Ponerinae* to deteriorate so rapidly as to become like that of the *Formicinae*, during the development of only one sub-family. In any case, where is the intermediate stage, if not represented by the *Dolichoderinae*?

Thus it seems certain that the *Dolichoderinae* developed from the *Ponerinae*, through the genera *Prolaneuretus* (fossil Ponerine) and *Aneuretus* (living *Dolichoderinae*). Also that the *Formicinae* developed from the primitive *Dolichoderinae*. We have therefore dealt with one complete branch of the phylogenetic tree, that which starts with the *Ponerinae*, and finishes with the most highly developed of the *Formicinae*, which are the most well developed of all the *Formicidae*.

To return to another branch, that which proceeds through the *Cerapachyinae* and *Dorylinae*. This branch finishes with the specialised sub-family *Leptanillinae*; on this I believe there is complete agreement. The third and last main branch of the tree, is that which develops into the *Myrmicinae*. The only disagreement concerning this branch is with regard to the method by which the *Myrmicinae* actually descended from the *Ponerinae*. FOREL believed that the *Myrmicinae* descended from the *Ponerinae* through the genus *Melapone*, this being contradicted by WHEELER. I agree with FOREL. The *Pseudomyrminae* branched off from the *Myrmicinae* very soon after the latter had evolved from the *Ponerinae* and, I believe, became a very specialised « dead end » of the tree.

It must be borne in mind that the process of evolution is still taking place; that the *Ponerinae*, as are all the rest of the sub-families, are still in existence and therefore adding new species; it being practically certain that new sub-families will eventually appear. This accounts for the fact that many genera do not appear to fit in with the phylogenetic tree. It is certain that the *Myrmicinae* did not develop until, the development of the *Dorylinae*, had started, if not finished. Only a few of the Myrmicine genera developing during the Mesozoic; on this both EMERY and WHEELER agree. The highly developed *Dolichoderinae* and the *Formicinae* did not develop until the early Tertiary

I have tried to be as concise as possible in this short paper, and hope that it will help to settle the doubt that must exist in some people's minds concerning this difficult and complicated question.



N. B. — The transverse line represents the end of the Mesozoic.

All sub-families are placed according to time of original development. This is necessitated because they are all in existence today.